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Constant Rate Harvesting of Populations Governed by Volterra Integral Equations

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1. The effect of removing members from a population at a constant time rate has been studied for population sizes which are modelled by ordinary differential equations [2]. Such models represent populations for which it is assumed that the time rate of growth of population depends only on the population size. A more realistic model also assumes a probability of death depending on age which leads to a Volterra integral equation. Such models have been considered for populations, as well as for the number of members of a given population who are afflicted with a disease, from which recovery confers no immunity against reinfection [1, 4]. In this paper we examine the effect of constant rate harvesting on such a model, and show that qualitatively the effect is similar to the effect of harvesting on an ordinary differential equation model. That is, there is a critical harvest rate which leads to extinction of the species, and for harvest rates less than the critical one it is possible to calculate the limiting population. The new feature of the more refined model considered here is that these calculations can be made directly in terms of observable parameters, rather than on such quantities as maximum unharvested growth rates which were used for calculation from the ordinary differential equation model in [2], and which are derived from computer simulations rather than directly from experiment.

2. We consider the Volterra integral equation

$$x(t) = f(t) + \int_0^t g(x(t-s))\,P(s)\,ds \tag{1}$$

as a representation of the size $x(t)$ at time t of a population whose growth rate depends only on the population size, and with a probability of death which depends only on age. Here, $g(x)$ is the number of members added to the

population in unit time when the population size is x, so that $g(x)/x$ is the rate of growth of population size in unit time per unit of population size. The function $P(t)$ represents the probability that a member of the population survives to age t, and the function $f(t)$ represents the number of members of the population who were already present at time $t = 0$ and who are still alive at time t.

In studying Eq. (1), we shall always make the following assumptions, the same as those made in [1], on the functions f, g, and P:

H_f: We assume that $f(t)$ is nonnegative, continuous and of bounded variation on $0 \leqslant t < \infty$, so that

$$f(\infty) = \lim_{t\to\infty} f(t)$$

exists.

H_p: We assume that $P(t)$ is nonnegative, monotone nonincreasing, and differentiable on $0 \leqslant t < \infty$, and is normalized so that $P(0) = 1$. We also assume

$$\int_0^\infty P(s)\, ds < \infty.$$

H_p: We assume that $g(0) = 0$, that $g(x)$ is continuous and non-negative on $0 \leqslant x < \infty$, and that $g'(x)$ is continuous on $0 \leqslant x < \infty$.

For a given value of $f(\infty)$, there is a set of functions $f(t)$ satisfying H_f and tending to this limit as $t \to \infty$. To each such $f(t)$ corresponds a unique solution of (1). When we speak of the collection of all solutions of (1), we shall mean the collection of solutions $x(t)$ corresponding to some such $f(t)$. We shall always assume that all nonnegative solutions of (1) are bounded on $0 \leqslant t < \infty$; sufficient conditions for this which appear to be plausible assumptions for many population growth problems, for example $\limsup_{x\to\infty} g(x)/x = 0$, are given in [1]. Observe that only nonnegative solutions are of interest as $x(t)$ is a population size.

To describe the size of a population under harvesting at a constant time rate E, we use the Volterra integral equation

$$x(t) = f(t) + \int_0^t g(x(t-s))\, P(s)\, ds - E\Phi(t), \tag{2}$$

where $E\Phi(t)$ represents the number of members harvested up to time t who would otherwise have survived to time t. Concerning the function Φ, we shall always make the following assumption

H_Φ: We assume that $\Phi(t)$ is non-negative, continuous, and of bounded variation on $0 \leqslant t < \infty$, so that

$$\Phi(\infty) = \lim_{t\to\infty} \Phi(t)$$

exists.

Since the hypotheses for $f(t)$ and $f(t) - E\Phi(t)$ are the same (the non-negativity is nonessential), all nonnegative solutions of (2) are bounded.

Obviously, the precise form of $\Phi(t)$ depends on the age distribution of the members of the population who are harvested. For example, if all members are harvested at age zero it is easy to calculate $\Phi(t) = \int_0^t P(s)\,ds$, so that $\Phi(\infty) = \int_0^\infty P(s)\,ds$. If the age distribution of the harvested members is the same as the age distribution of a time-independent population, which would appear to be a plausible hypothesis for many problems in which the total population and the harvesting rate are both large, then we can give an explicit expression for $\Phi(t)$.

THEOREM 1. *Suppose that at any time the number of members of age u harvested is proportional to $P(u)$. Then the number of members harvested who would otherwise have survived until time t is*

$$E\Phi(t) = E\,\frac{\int_0^t uP(u)\,du}{\int_0^\infty P(u)\,du}. \tag{3}$$

In particular, $\Phi(\infty) = \sigma$, the average age of the population, defined by

$$\Phi(\infty) = \sigma = \frac{\int_0^\infty uP(u)\,du}{\int_0^\infty P(u)\,du}. \tag{4}$$

Proof. The fraction of the population of age u in a stable population distribution is $P(u) \mid \int_0^\infty P(u)\,du$; hence the number harvested at time s of age u is $EP(u)/\int_0^\infty P(u)\,du$. Since the probability at time s of survival of each member of age u until time t, that is until age $t - s + u$, is $P(t - s + u)/P(u)$, the number harvested at time s of age u who would otherwise have survived until time t is $EP(t - s + u)/\int_0^\infty P(u)\,du$. Thus the number harvested at time s (of all ages) who would otherwise have survived to time t is $E\int_0^s P(t - s + u)\,du/\int_0^\infty P(u)\,du$, and the total number harvested at all times up to t who would otherwise have survived is

$$E\int_0^t \left[\int_0^s P(t - s + u)\,du\right] ds \Big/ \int_0^\infty P(u)\,du.$$

We now obtain

$$\Phi(t)\int_0^\infty P(u)\,du = \int_0^t \left[\int_0^s P(t-s+u)\,du\right] ds$$

$$= \int_0^t \left[\int_{t-s}^t P(v)\,dv\right] ds$$

$$= \int_0^t \left[\int_{t-v}^t P(v)\,ds\right] dv = \int_0^t vP(v)\,dv,$$

which implies (3) and (4), as desired.

By the same type of computation we may establish the following result for an arbitrary age distribution of harvested members.

COROLLARY. *Suppose that at any time the number of members of age u harvested is* $E\alpha(u)$, *where* $\int_0^\infty \alpha(u)\,du = 1$. *Then the corresponding term* $\Phi(t)$ *in Eq.* (2) *is given by*

$$\Phi(t) = \int_0^t \left[\int_0^v \frac{\alpha(u)}{P(u)}\,du\right] P(v)\,dv,$$

and

$$\Phi(\infty) = \int_0^\infty \left[\int_0^v \frac{\alpha(u)}{P(u)}\,du\right] P(v)\,dv.$$

The case of an age distribution of harvested members which varies with the time may also be treated, but in order to deal with it, it is necessary to assume the existence of a limiting age distribution as the harvesting time becomes large.

The question of whether every bounded solution of (1) tends to a limit as $t \to \infty$ has been studied extensively; see for example [5, 9, 11]. For example, we quote the following result, actually established under less stringent hypotheses.

THEOREM 2 (London [9]). *Suppose the conditions* H_f, H_P, H_g *are satisfied. Then every bounded solution* $x(t)$ *of* (1) *satisfies*

$$\lim_{t\to\infty}\left[x(t) - g(x(t))\int_0^\infty P(s)\,ds\right] = f(\infty).$$

It is easy to see that if $x(t)$ is a solution of (1) with $\lim_{t\to\infty} x(t) = x_\infty$, then

$$\lim_{t\to\infty}\int_0^t g(x(t-s))\,P(s)\,ds = g(x_\infty)\int_0^\infty P(s)\,ds.$$

It follows that the limit x_∞ must satisfy the equation

$$x_\infty = f(\infty) + g(x_\infty) \int_0^\infty P(s)\, ds. \tag{5}$$

If the roots of Eq. (5) are isolated, then it follows from Theorem 2 that every bounded solution of (1) tends to a limit x_∞ which is a root of (5). In other words, the possible limits of solutions of (1) are given by the abscissae of the intersections of the curve $y = g(x)$ and the straight line $y = [x - f(\infty)]/[\int_0^\infty P(s)\, ds]$. If $f(\infty) = 0$, then $x_\infty = 0$ is the abscissa of an intersection, while if $f(\infty) > 0$ but $g(x)$ grows more slowly than x as $x \to \infty$ (which guarantees boundedness of solutions of (1)), then there is an intersection with $x > 0$.

If $\Phi(t)$ satisfies the hypothesis H_Φ, then Theorem 2 may be applied to Eq. (2). However, since $f(\infty) - E\Phi(\infty)$ is negative for sufficiently large E, there may be no intersections of the curve $y = g(x)$ with the line $y = [x - f(\infty) + E\Phi(\infty)]/[\int_0^\infty P(s)\, ds]$ in the first quadrant of the x–y plane. The line may lie above the curve for all x. Since all nonnegative solutions of (2) are bounded, and since by Theorem 2 all bounded solutions tend to limits which are intersections of the curve and line, it follows that if the curve and line do not intersect then every solution becomes negative, and hence reaches zero in finite time.

The analog of Theorem 2 for Eq. (2) is the following result

THEOREM 3. *Suppose that the conditions* H_f, H_P, H_g, *and* H_Φ *are satisfied. Suppose also that the roots of the equation*

$$x_\infty = f(\infty) + g(x_\infty) \int_0^\infty P(s)\, ds - E\Phi(\infty) \tag{6}$$

are isolated. Then every bounded nonnegative solution of (2) *either tends to a root of* (6) *as* $t \to \infty$ *or reaches zero in finite time.*

The question that we wish to study is how the limit x_∞ of a solution of (2) depends on the harvesting rate E. In view of Theorem 3, this reduces to the questionof solving Eq. (6) for x_∞ as a function of E, which may be answered immediately by application of the implicit function theorem. We obtain the following result.

THEOREM 4. *Let* $x(t)$ *be a solution of* (1) *which tends to the limit* $x_\infty(0)$ *as* $t \to \infty$, *and suppose that*

$$g'(x_\infty(0)) \int_0^\infty P(s)\, ds \neq 1. \tag{7}$$

Then there is an interval of values $0 \leqslant E < E_c$ *on which the limit* $x_\infty(E)$ *of the solution of* (2) *depends continuously and differentiably on* E, *with*

$$\frac{dx_\infty(E)}{dE} = \frac{-\Phi(\infty)}{1 - g'(x_\infty(E)) \int_0^\infty P(s)\, ds}. \tag{8}$$

The critical harvest E_c *is defined by*

$$g'(x_\infty(E_c)) \int_0^\infty P(s)\, ds = 1. \tag{9}$$

If $E_c < \infty$, *then* $x_\infty(E)$ *has a discontinuity at* E_c, *except possibly if* $g''(x_\infty(E_c)) = 0$.

Geometrically, we find $x_\infty(E)$ by finding the abscissa of the intersection of the curve $y = g(x)$ and the straight line $y = [x - f(\infty) + E\Phi(\infty)]/[\int_0^\infty P(s)\, ds]$. As E increases, the line moves up, and if $g'(x_\infty(E)) \int_0^\infty P(s)\, ds = 1$, the line is tangent to the curve. A further increase in E causes the disappearance of an intersection, unless the curve has an inflexion point at the point of tangency, with the result that either $x_\infty(E)$ must jump to a different intersection or $x(t)$ must reach zero in finite time. Such an occurrence is called a catastrophe in the mathematical sense, because it corresponds to a biological catastrophe such as a sharp change in the equilibrium population, or even the extinction of the species if the critical harvest E_c is exceeded. However, if (1) is used as a model for the number of members of a given population with a disease, then E_c represents the rate at which members must be cured, or at least quarantined from the rest of the population, to assure eradication of the disease in finite time.

It may be observed from (8) that if $g'(x_\infty(0)) \int_0^\infty P(s)\, ds > 1$, then an increase in the harvesting rate produces an increase in the limiting population. This appears unrealistic and in fact, it will be shown in another paper that an equilibrium x_∞ with $g'(x_\infty) \int_0^\infty P(s)\, ds > 1$ is unstable in the sense that a small perturbation of the integral equation may produce a large change in the solution. Thus it would seem reasonable to require $g'(x_\infty) \int_0^\infty P(s)\, ds < 1$ instead of (7) in Theorem 4 if the equation (2) is to describe a real population.

3. As an example of the application of the results of the preceeding section to a real population problem, we examine the dynamics of the population of sandhill cranes (Grus canadensis) as studied by R. S. Miller and D. B. Botkin [10]. This was also examined in [2] using a logistic model with coefficients calculated from the observed equilibrium population and the maximum unharvested growth rate. This maximum unharvested growth rate was estimated from the computer simulation of [10], rather than being obtained directly from observations. Here we use the coefficients used to

construct the computer simulation in [10] and Theorems 3 and 4 to make predictions comparable to some of those in [10].

In [10] it was postulated that the number of members added to the population in unit time is

$$g(x) = R_0 x e^{-kx}, \tag{10}$$

with

$$R_0 = 0.15, \qquad k = 3.48 \times 10^{-6}. \tag{11}$$

Since sandhill crames are assumed to have a maximum lifetime of 25 years, we take $f(\infty) = 0$. From (5), it follows that the recruitment rate at equilibrium, $g(x_\infty)/x_\infty$, is equal to $1/[\int_0^\infty P(s)\,ds]$; this rate was taken in [10] to have the value 0.076, which yields

$$\int_0^\infty P(s)\,ds = 13.16. \tag{12}$$

The data on mortality rates in [10] is not in the most suitable form for the calculation of $\int_0^\infty P(s)\,ds$ and σ, and for this reason we have chosen to use (12), and to treat the graph of $P(t)$ as if it were a straight line decreasing from the value 1 at $t = 0$ to the value zero in such a way that the equation (12) holds. Then $P(u) = 1 - (u/2A)$ $(0 \leqslant u \leqslant 2A)$, $P(u) = 0$ $(u > 2A)$, where $A = \int_0^\infty P(u)\,du = 13.16$, and $\sigma = (1/A)\int_0^{2A} u(1 - (u/2A))\,du = \frac{2}{3}A$, or

$$\sigma = 8.77. \tag{13}$$

We begin by calculating $x_\infty(0)$ from (5), using $f(\infty) = 0$, (10), (11), and (12). This gives

$$x_\infty(0) = \frac{1}{k}\log\left(R_0\int_0^\infty P(s)\,ds\right) = 195{,}400,$$

which is consistent with the observed value of 194,600. We remark that one reason for discarding the data on mortality rates in [10] is that it appears to give a larger value of $\int_0^\infty P(s)\,ds$ and a correspondingly larger value of $x_\infty(0)$. For our purposes, calculation of the best values of the coefficients should require consistency between $\int_0^\infty P(s)\,ds$, the recruitment rate at equilibrium, and the equilibrium population.

The next step is to calculate $x_\infty(E_c)$ from (9). Because of (10), this reduces to the solution of

$$R_0\int_0^\infty P(s)\,ds(1 - kx_\infty(E_c)) = e^{kx_\infty(E_c)}. \tag{14}$$

Using (11) and (12) in (14), we obtain

$$x_\infty(E_c) = 89{,}000. \tag{15}$$

Now we obtain E_c from (6), which here takes the form

$$\Phi(\infty)\, E_c = R_0 \int_0^\infty P(s)\, ds x_\infty(E_c)\, e^{-kx_\infty(E_c)} - x_\infty(E_c).$$

The assumption that the age distribution of harvested birds is proportional to the age distribution of the total population gives $\Phi(\infty) = \sigma$, and now (11), (12), (13), and (15) give $E_c = 4{,}550$.

We may also calculate the equilibrium population corresponding to any harvest rate $E < E_c$ by means of (6). The results, together with those of [10] and [2] are given in Table I.

TABLE I

E	$x_\infty(E)$	$x_\infty(E)$ from [10]	$x_\infty(E)$ from [2]
2,000	166,700	167,500	171,600
3,000	148,600	149,900	156,900
4,000	123,800	125,800	137,000

The calculation of extinction times for values of $E > E_c$ for this model is considerably more difficult than for the logistic model of [2]. Such information could be obtained by numerical approximation of the solution of (2) for a given value of E.

4. Another type of harvesting which may be of interest is where the harvesting rate at any time is proportional to the population at that time. Such problems have been studied, for example, for operation of commercial fisheries [3]. If the harvesting rate at time t is $Ex(t)$, $(0 \leqslant E \leqslant 1)$, the same arguments used to derive Eq. (3) give an equation

$$x(t) = f(t) + \int_0^t g(x(t-s))\, P(s)\, ds - E\Phi(t)\, x(t). \tag{16}$$

The change of variable $y(t) = x(t)\,[1 + E\Phi(t)]$ transforms (16) into an equation of the form

$$y(t) = f(t) + \int_0^t h(s, y(s))\, P(t-s)\, ds$$

with $h(s, y) = g(y/[1 + E\Phi(s)])$ for each y. It is possible to show the existence of a limit x_∞ for any bounded solution of (16), and any limit x_∞ must satisfy

$$x_\infty(1 + E\Phi(\infty)) = f(\infty) + g(x_\infty) \int_0^\infty P(s)\, ds. \tag{17}$$

Just as for constant rate harvesting considered in Section 2, it appears reasonable to require

$$g'(x_\infty) \int_0^\infty P(s)\, ds < 1 \tag{18}$$

to assure stability of (18) under small perturbations. Since application of the implicit function theorem shows that (17) can be solved for x_∞ as a function of E unless $1 - g'(x_\infty) \int_0^\infty P(s)\, ds + E\Phi(\infty) = 0$, the requirement (18) assures that there is no mathematical catastrophe. That is, x_∞ depends continuously on E for all E, $0 \leqslant E \leqslant 1$. However, there remains the possibility of a biological catastrophe, indicated by $x_\infty(E) = 0$. If $f(\infty) > 0$, it is clear that $x_\infty = 0$ is not a solution of (17). On the other hand, if $f(\infty) = 0$, then we may easily see from (17) that $\lim_{E \to E_c} x_\infty(E) = 0$ if E_c is defined by

$$E_c = \frac{g'(0) \int_0^\infty P(s)\, ds - 1}{\Phi(\infty)}. \tag{19}$$

Thus if $1 < g'(0) \int_0^\infty P(s)\, ds < 1 + \Phi(\infty)$, there is a critical harvest E_c, $0 < E_c < 1$, given by (19) for which $x_\infty(E_c) = 0$. Proportional harvest rates $E > E_c$ will lead to extinction also, since they would produce negative limiting populations.

For the sandhill crane model considered in Section 3, with $g(x) = R_0 x e^{-kx}$, $R_0 = 0.15$, $\int_0^\infty P(s)\, ds = 13.16$, and $\Phi(\infty) = \sigma = 8.77$, calculation from (19) gives a critical proportional harvesting rate of 0.111.

5. These is no theoretical difficulty in extending the models considered here to multispecies problems involving competition between species. However, even for two species, explicit formulae would be very difficult to obtain. For predator–prey problems, a different model would be required in which prey who dies naturally are distinguished from prey who are killed by predators. While both competition and predator–prey models of Volterra integral equation type would be interesting, and perhaps useful, there appear to be significant difficulties, both theoretical and computational, in their study.

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